Internal conductance of Scots pine varies with atmospheric moisture

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Introduction

Carbonyl sulfide (COS) measurements can be used to compute stomatal and internal conductance to COS of plants as COS uptake in leaves is a one-way flux and does not require light, in contrast to photosynthesis. The possibility to separate the stomatal conductance ($g_{s,COS}$) from the full conductance pathway leaves the ability to study the internal conductance to COS ($g_{i,COS}$). $g_{i,COS}$ comprises the combined mesophyll (g_m), chloroplast membrane (g_{ch}) and biochemical ($g_{bch,CA}$) conductances of COS (Fig 1).
The main goal of this study was to identify environmental drivers of the internal conductance to COS which was never done before, especially using carbonyl sulfide flux data.
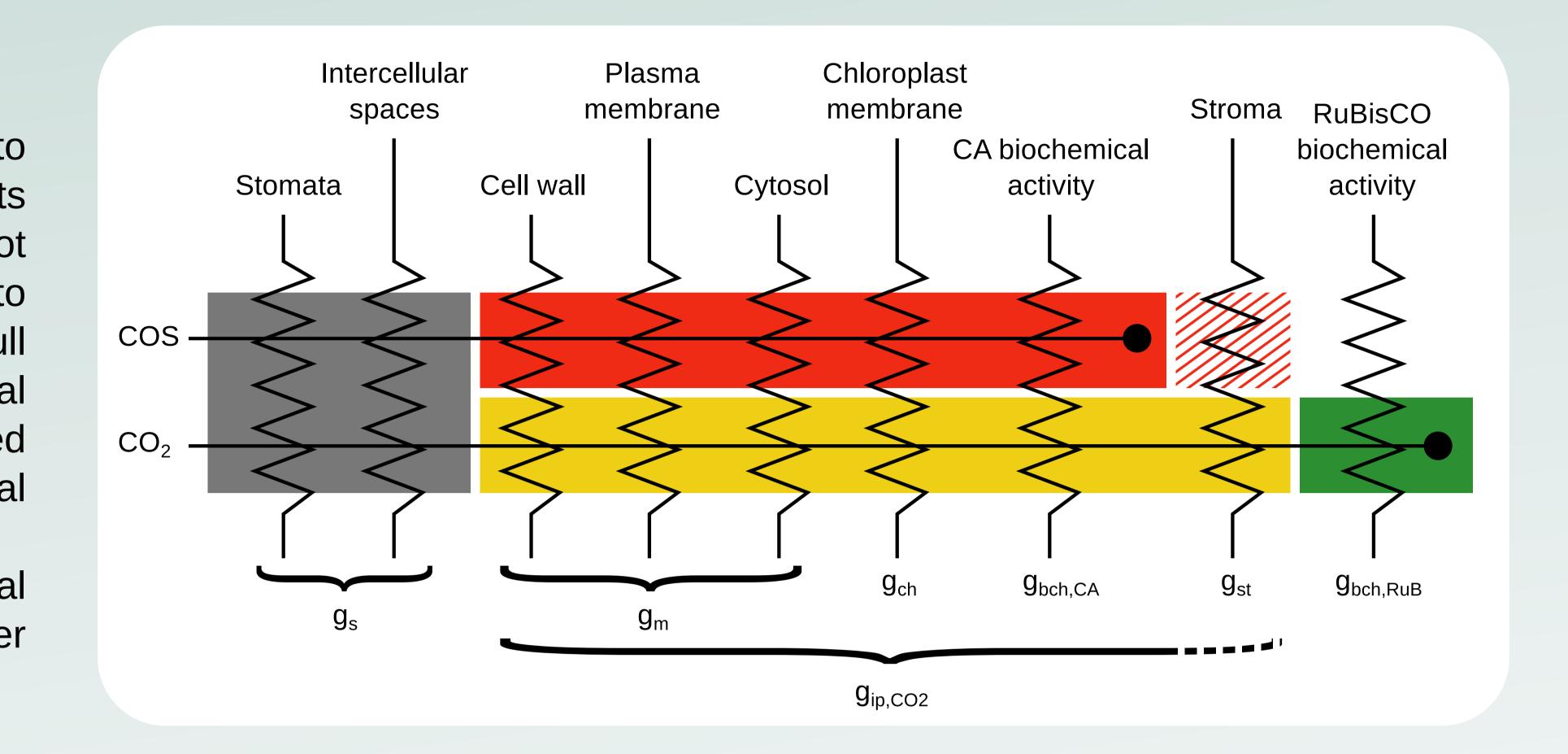

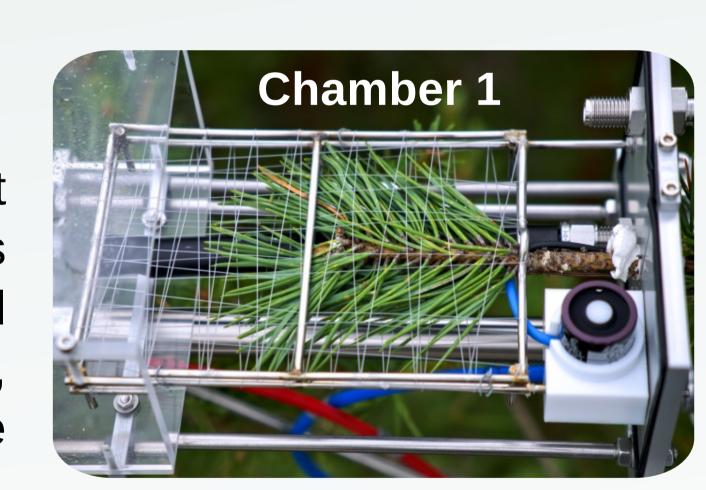**Fig. 1 Scheme of COS and CO_2 diffusion pathways**

Conductances denoted in the scheme are: g_s – stomatal (stomata and intercellular spaces, grey area), g_m – mesophyll (cell wall, plasma membrane and cytosol), gch – chloroplast membrane, g_{st} – chloroplast stroma, $g_{bch,CA}$ – biochemical capacity of carbonic anhydrase (CA) located at inner side of chloroplast membrane, where majority of COS is decomposed (Stimler et al. 2010). Red area represents the internal conductance of COS ($g_{i,COS}$). Part of CA is also located in stroma, and therefore gst also contributes in part to $g_{i,COS}$. CO_2 equivalent of $g_{i,COS}$ represents partial internal conductance to CO_2 ($g_{ip,CO2}$). Yellow area represents internal conductance of CO_2 ($g_{i,CO2}$), which, in addition to being a part of the stroma resistance, is equal to $g_{i,COS}$. The green area representing the biochemical activity of RuBisCO ($g_{bch,RuB}$) is not involved in $g_{i,CO2}$.

Methods

Station for Measuring Forest Ecosystem – Atmosphere Relations (SMEAR II) in Hyytiälä, Finland (61°51′ N, 24°17′ E, 181 m a.s.l.), which is dominated by Scots pine (*Pinus sylvestris* L.).

Dendrometers were used to measure xylem diameter changes, which has been shown to be proportional to changes in water potential (WPP).

Air temperature (Ta), relative humidity (RH), vapor pressure deficit (VPD), water vapor fluxes (F_{H2O}) and photosynthetically active radiation (PAR) were also measured.

Chamber 1
Chamber 1
Chamber 2

Fig 2: Two automated leaf gas-exchange chambers were installed at the top of the canopy in one Scots pine tree. The chambers were of a different type with different spacing of the needles.

Ball-Berry model (Ball et al. 1987) was used to obtain g_s to water vapor, which was then converted to g_s to COS ($g_{s,COS}$). The parameters of empirical slope and intercept were determined from g_s, which was computed using F_{H2O} and VPD during lower RH conditions, RH < 70% (Kooijmans et al. 2018).

With assumptions that boundary layer conductance is negligible (ventilated chambers) and concentration of COS inside chloroplasts is near zero (COS is fully destroyed), we computed the internal conductance of COS from COS flux (F_{COS}), ambient COS concentration ($C_{a,COS}$) and $g_{s,COS}$ as follows (Seibt et al. 2010, Wehr et al. 2017):

$$g_{i,COS} = \frac{F_{COS} \cdot g_{s,COS}}{-C_{a,COS} \cdot g_{s,COS} - F_{COS}}$$

Results and discussion

Univariate dependencies of $g_{i,COS}$ on Ta, RH, PAR, VPD, WP and F_{H2O} were analysed to examine whether $g_{ip,CO2}$ is reflecting micrometeorological conditions, tree water status and transpiration rate.

We observed the strongest dependency on VPD and RH, weaker dependency is apparent also on Ta and WPP (in averages from both chambers). The $g_{ip,CO2}$ did not seem to reflect the F_{H2O} at all in chamber 2. There was a weak dependence observed in chamber 1, which is an artefact caused by filtering out the high RH data, done only in chamber 1 (Fig 3).
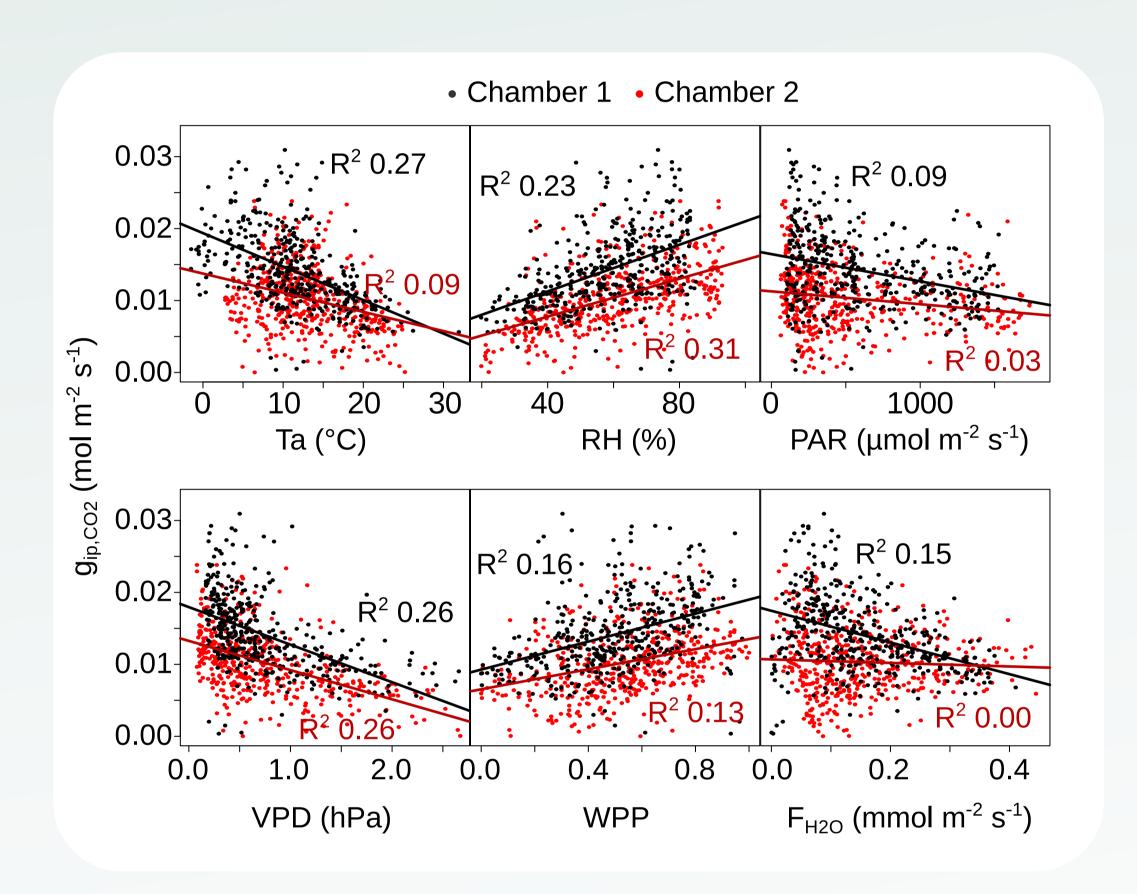

Fig 3: Univariate dependencies in chamber 1. R^2 - coefficient of determination of linear regression

Multivariate dependencies of all six variables were tested for significance. We considered nonlinear relationships with $g_{ip,CO2}$, interactions up to up to 3rd degree of combinations of all variables and used non-parametric regression method (MARS) to be sure that inter-correlated drivers would not increase explanatory strength artificially.
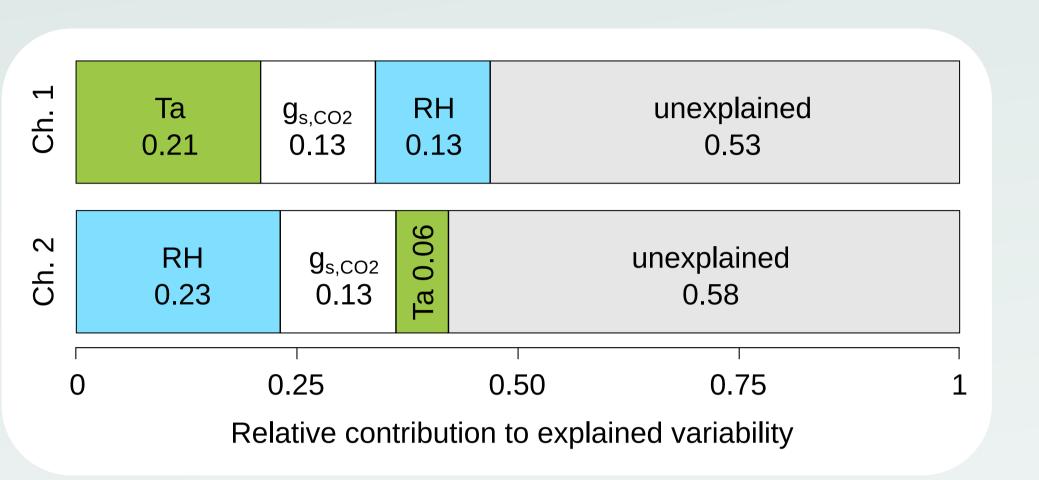

Fig 4: Relative contribution of each variable to explained variability of $g_{ip,CO2}$

The full set of variables explained 62% and 51% of variability in $g_{ip,CO2}$ in chambers 1 and 2 respectively. **Ta, RH and $g_{s,CO2}$ solely can explain the most of variability** in chamber 1 and 2 (47% and 42% respectively, Fig 4).

PAR, WPP and F_{H2O} are not important drivers of $g_{ip,CO2}$. **VPD can be explained by Ta and RH** by definition.

Less explained variability in chamber 2 suggests that the differences in leaf arrangement had an impact on the response of leaves to environmental conditions.
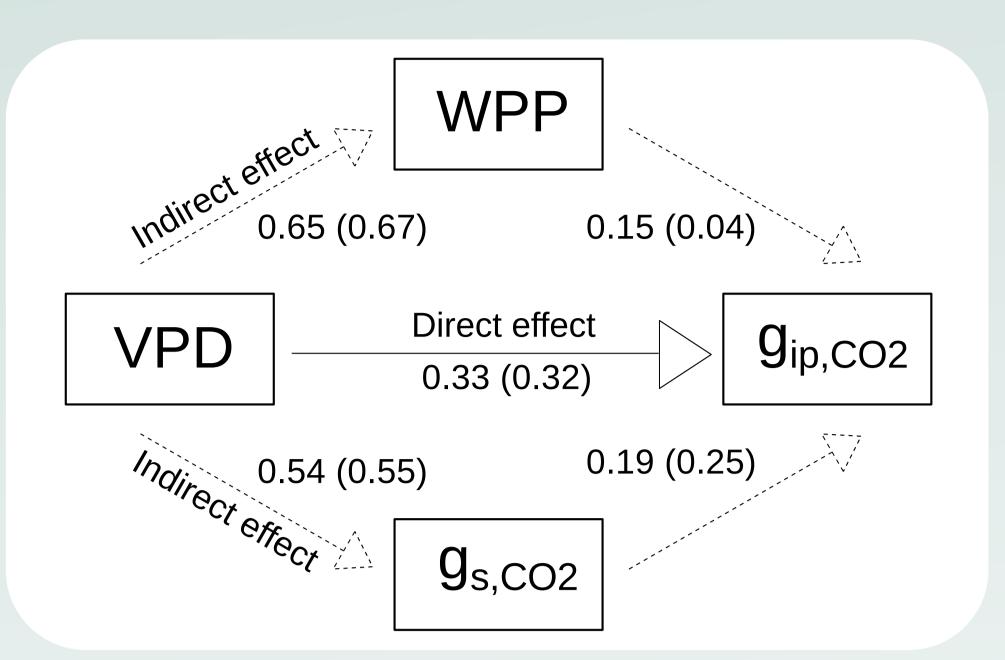

Fig 5: Diagram of the path analysis

We employed the path analysis to determine the causality of the relationships obtained from single- and multivariate analysis - the **dependence of $g_{ip,CO2}$ on VPD**.

It is not evident, whether the $g_{ip,CO2}$ × VPD dependency is caused by the direct VPD impact or indirect through other variables, i.e. WPP or $g_{s,CO2}$ (Fig 5).

The direct effect of VPD is the strongest one (Tab 1), however, it is hard to explain the mechanism. It could be caused by leaf osmolality (as a function of water and sugar content) or water potential (our proxy might not be good enough).

Tab 1: Results of path analysis

	Direct effect	Indirect effect ($g_{s,COS}$)	Indirect effect (WPP)	Total effect (R^2)
Chamber 1	0.33	0.10	0.10	0.53
Chamber 2	0.32	0.14	0.03	0.49

References

Ball, J. T., Woodrow, I. E. & Berry, J. A. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: Biggens, J. (Ed.), Progress in Photosynthesis Research, vol. IV. 221-224 (1987)

Seibt, U., Kesselmeier, J., Sandoval-Soto, L., Kuhn, U. & Berry, J. A. A kinetic analysis of leaf uptake of COS and its relation to transpiration, photosynthesis and carbon isotope fractionation. Biogeosciences 7, 333-341, doi:10.5194/bg-7-333-2010 (2010)

Wehr, R. et al. Dynamics of canopy stomatal conductance, transpiration, and evaporation in a temperate deciduous forest, validated by carbonyl sulfide uptake. Biogeosciences 14, 389-401, doi:10.5194/bg-14-389-2017 (2017)

Kooijmans, L. M. J. et al. Influences of light and humidity on carbonyl sulfide-based estimates of photosynthesis. PNAS, online (2019)

Abbreviations

CA ... carbonic anhydrase
$C_{a,COS}$ ... ambient concentration of COS
F_{H2O} ... water vapor flux
F_{COS} ... carbonyl sulphide flux
$g_{bch,CA}$ ... biochemical capacity of CA
$g_{bch,RuB}$ ... biochemical capacity of RuBisCO
g_{ch} ... cloroplast membrane conductance
$g_{i,COS}$ ... internal conductance to COS
$g_{i,CO2}$ ... internal conductance to CO_2
$g_{ip,CO2}$ ... partial internal conductance to CO_2
g_m ... mesophyll conductance
g_s ... stomatal conductance
$g_{s,COS}$ ... stomatal conductance to COS
g_{st} ... chloroplast stroma conductance
PAR ... photosynthetically active radiation
RH ... relative air humidity
Ta ... air temperature
VPD ... vapor pressure deficit
WPP ... leaf water potential proxy